

III.—On Larvæ of *Lingula* and *Pelagodiscus* (*Discinisca*). By J. H. Ashworth,
D.Sc., Lecturer in Invertebrate Zoology in the University of Edinburgh.*

(Received March 15, 1915. Read March 15, 1915. Issued separately November 19, 1915.)

[Plates IV and V.]

C O N T E N T S.

	PAGE		PAGE
The Larvæ of <i>Lingula</i>	46	Comparison of the Larvæ with those pre-	
Previous Records of the Larvæ of <i>Lingula</i>		viously recorded	54
(<i>s. lat.</i>)	46	Breeding Seasons	56
The Larvæ of <i>Lingula anatina</i>	47	Comparison of the Larvæ of <i>Lingula anatina</i>	
Localities	47	with Brooks's Larvæ of <i>Glottidia audebarti</i>	56
Description of the Larvæ	47	The Larvæ of <i>Pelagodiscus</i> (<i>Discinisca</i>)	58
(i) Larvæ with 8-10 pairs of Cirri	47	Previous Records of the Larvæ of <i>Discinidæ</i>	58
(ii) " 11 "	49	The Larvæ of <i>Pelagodiscus</i> (<i>Discinisca</i>) <i>atlanticus</i>	59
(iii) " 12 "	49	Description of the Larvæ	60
(iv) " 13 "	50	List of Literature	66
(v) " 14-15 "	52	Description of the Plates	67

The specimens which form the subject of this paper were collected on voyages to and from Australia on board the s.s. *Orsova* and *Otway* of the Orient Line. Sea-water was being constantly pumped on each ship, by a rotary pump, from an inlet about 18 feet below the water-line to a large tank on the boat deck, and I was allowed to run off, through a plankton net, as much of the water as I desired in order to collect the organisms contained therein. For this privilege, of which I availed myself to a liberal extent, I beg to thank Captain J. F. HEALEY and Captain F. S. SYMONS. The small organisms suffered comparatively little by their passage through the pump and pipes, and were, for the most part, in a living and active condition when examined.

The larvæ of *Lingula* have been so seldom recorded that the occurrence of fourteen larvæ of *Lingula anatina* in the catch made on June 21, 1914, in the southern part of the Red Sea, was noteworthy. On the return journey, in October, careful watch was kept for others, and one larva of *Lingula anatina* was taken in the Indian Ocean, about 4° south of Colombo, two others in the southern portion of the Red Sea, and six larvæ of *Pelagodiscus* (*Discinisca*) a little to the west of Cape Comorin. The larvæ were examined microscopically immediately after capture, and were then preserved in formalin, which has proved to be a satisfactory fixative. Most of the specimens have been stained in hæmatoxylin, cleared, and mounted as whole objects, for which their depressed form and transparent shell and mantle render them very suitable; six larvæ have been cut into serial sections.

* A grant in aid of the expenses incurred during this research has been received from the Earl of Moray Endowment of the University of Edinburgh. The cost of reproduction of the plates has been defrayed by the Carnegie Trust for the Universities of Scotland.

THE LARVÆ OF LINGULA.

PREVIOUS RECORDS OF THE LARVÆ OF LINGULA (S. LAT.).

(a) *Lingula anatina* Bruguière.—The larva of *Lingula* was first observed by SEMPER (1861), who, in 1859, saw a free-swimming larva, without stalk, near Zamboanga, Mindanao (Philippine Islands). Later (1864) he obtained several other specimens, which fixed themselves in his aquaria and lived several weeks. SEMPER gives no further information about his specimens, but no doubt they were larvæ of *L. anatina*, for this species was found in hundreds on the beach at Zamboanga by the *Challenger* Expedition.

Dr YATSU (1902), while working at Misaki in Japan, obtained the fertilised eggs of *L. anatina*, and has given a detailed account of the egg-cleavage and of the larvæ. Captain SEWELL (1912) published a short note on larvæ, which he refers to this species, from the coast of South Burma.

(b) *Glottidia audebarti* (Broderip) = *Lingula pyramidata* Stimpson.—Early in June 1860 M^cCRADY found in Charleston Harbour, South Carolina, a free-swimming larva, and gave an account of it to the Elliott Society of Natural History on June 15, which, however, was never published by the Society owing to the destruction during the war of the notes and drawings of the larva. There is, in a letter written by M^cCRADY (1860) to STIMPSON on June 18, 1860, a brief description of the larva, and M^cCRADY subsequently wrote from memory a further report upon it, which was given to and published by Professor MORSE (1873, p. 261). M^cCRADY, who believed his specimen to be the young of "*Lingula pyramidata*," states that it had about 6* pairs of cirri, and that there was no trace of peduncle, but his description shows that what he regarded as the intestine was undoubtedly the peduncle, which was evidently of considerable length and convoluted.

BROOKS (1879), who was the first to study a series of larvæ of "*Lingula*," published an excellent account of the structure of the larvæ of "*L. pyramidata*," which he obtained in Chesapeake Bay (see pp. 56, 57).

(c) *Species unknown*.—Professor SIMROTH (1897, p. 6), has recorded a larva with 10 pairs of cirri among the material obtained by the Plankton Expedition from the west coast of Africa. The larva was .66 mm. in transverse diameter, and had no stalk. In its general structure and in the shape and dimensions of its shell this larva approaches that of *Lingula anatina*, but the hinge-line is about one-fifth shorter than in the larvæ studied by Dr YATSU and myself, and the protegulum is also proportionately smaller. The shell of Professor SIMROTH's larvæ is much larger than that of the corresponding stage of *Glottidia* as described by BROOKS, and is of different shape; the hinge-line is one and a half times as long, and the protegulum is larger in a similar proportion. This larva, therefore, does not agree with either of

* The number of cirri is probably considerably understated.

those of known parentage, though it is nearer to that of *Lingula anatina*, and should probably be referred to this genus. I am not aware of a record of adult specimens of any species of *Lingula* from the west coast of Africa, so that no clue to the species of Professor SIMROTH's larva can be obtained.

THE LARVÆ OF LINGULA ANATINA.

Localities.

The localities at which the larvæ were obtained may be stated thus:—

(i) Southern portion of the Red Sea, about lat. 15° N., long. 42° E.; June 21, 1914; depth of water about 16 to 40 fathoms; fourteen larvæ.

(ii) Indian Ocean, about lat. 3° N., long. 80° E.; October 14, 1914; depth of water about 2200 fathoms; one larva. The noteworthy feature about the record from this locality is the great depth of water in and all round the area where the larva was obtained, the nearest shallow water being that on the coast of Ceylon, distant some 200 miles north. *Lingula* is generally found between tide-marks or in shallow water.

(iii) Southern portion of the Red Sea, near the edge of the Dahalak Bank in lat. about 16° N.; October 22, 1914; depth of water about 30 fathoms, but there were shallow areas of about 7–9 fathoms within a few miles; two larvæ.

So far as I am aware, *Lingula* has not been recorded from the Red Sea, and the only recorded examples from the Indian Ocean are from the coast of Burma. Dr ANNANDALE tells me that he has seen *Lingula* in abundance on the islands off the Siamese state of Trang, on the west coast of the Malay Peninsula, and that there are specimens in the Indian Museum, Calcutta, from the Andaman Islands and the coast of Burma.

Description of the Larvæ (Plate IV).

It is not proposed to give a detailed description of the larvæ, as they agree in general with the excellent account given by Dr YATSU, but attention will be drawn to their principal features, and to certain points in which my larvæ differ from those studied by previous observers.

The specimens may be divided into five groups, according to the number of their cirri, which is probably the most reliable indication of the age of the larvæ.

(i) *Larvæ with 8–10 pairs of cirri.*—The youngest stage obtained was taken in the Indian Ocean (locality (ii)), about 4° nearly due south of Colombo. The shell-valves are .52 mm. long and .62 mm. broad, and have the form shown in figs. 1, 2. The straight hinge-line* is .3 mm. long, and the distance between the

* The cuticular shell first formed over the dorsal and ventral mantle-folds of the larva is circular in outline (YATSU); a large fold is formed posteriorly which divides the shell into dorsal and ventral valves or protegula (BEECHER). The valves increase in thickness, and later, as the secondary shell is added, in size; but the fold, as it is no longer in contact with the mantle, remains a mere film of cuticle, which, however, serves for some time as a hinge

tips of the teeth which lie right and left of the hinge-line on the ventral valve is .32 mm. These measurements remain unchanged throughout larval life, for subsequent additions to the valves take place on their lateral and anterior margins only. The straight hinge-line, in all the later stages examined, is about .28 to .32 mm. long (average of the whole series, .295 mm.), there being some individual variation.

The margins of the primary shells, or protegula,* are well seen in the dorsal and ventral valves, but especially in the latter, and remain recognisable in all the later larval stages examined. The two protegula are unequal; the dorsal one (fig. 2) is almost, but not quite, a semicircle of which the hinge-line, .3 mm. long, is the diameter, its length or height being .14 mm.; the ventral one is smaller (fig. 1), its length being .12 mm. When the formation of the secondary shell takes place, by additions to the lateral and anterior margins of the protegula, the two valves soon become approximately equal in size. In all my larvæ the two valves are either equal in size or the ventral one is slightly larger, as it is in the adult.

This larva has 8 pairs of ciliated cirri. The most anterior cirrus of each side is smaller than the rest, and has been recently formed; it lies immediately lateral to the base of the median sensory tentacle. This tentacle is an outgrowth from the lip-like fold (epistome) which overhangs the mouth in front.

The mouth leads into the œsophagus and mid-gut. The mid-gut is a wide sac, from the walls of which the lobes of the digestive gland or liver—a right and left posterior dorsal and a bifid ventral lobe†—are being formed. The intestine is only feebly differentiated, and the anus is not yet present. The anterior ocluser muscles are of moderate size, but the posterior ocluser has not yet appeared.

Two statocysts‡ are present in the dorsal body-wall, each situated a little posterior and median to the ocluser muscle of its side (see below, p. 51).

The organs practically fill the coelom, there being usually only small portions of the cavity recognisable right and left of the œsophagus and in the middle line at the posterior end.

There is no trace of peduncle. In regard to its internal organs, this larva has reached a stage of development similar to the larva with 5 pairs of cirri, represented in Dr YATSU's figs. 77, 78.

for the valves. In the specimen .52 mm. long, described above, the dorsal and ventral valves are still connected together posteriorly by the fold. In all the later stages examined, the fold, while remaining attached to the ventral valve, has become disconnected from the dorsal valve; it still, however, bends over dorsally so that its edge often engages with the now thickened, straight, posterior margin of the dorsal valve. This margin, which corresponds with that of the ventral valve, is the hinge-line referred to above.

* See footnote on previous page.

† For details of these lobes, see p. 52.

‡ Statocysts were first seen in Brachiopods by FRITZ MÜLLER (1860, p. 77), who observed them in larvæ of *Pelagodiscus*. Professor MORSE (1878, p. 266) recorded the presence of statocysts in adult *Lingula*, and BROOKS (1879, p. 63) saw them in larvæ of *Glottidia*. Professor BLOCHMANN (1898, p. 422; 1900, p. 124), however, denied the presence of statocysts in both *Lingula* and *Pelagodiscus*, and considered the structures in question to be the funnels of the nephridia. Dr YATSU (1902, pp. 64-68) held that they were statocysts, and, after having examined these organs in living and preserved specimens of both *Lingula* and *Pelagodiscus*, I can fully confirm his view. The funnels of the nephridia have a totally different appearance and different relations (see figs. 8, 10).

A larva with 10 pairs of cirri was taken in the Red Sea at locality (i). Its shell-valves are .76 mm. long, and .81 mm. broad, and the internal organs are similar to those of the larva with 8 pairs of cirri described above, except that the cœlomoduets (or nephridia; see below, p. 52) are now formed, and the liver-lobes and intestine more clearly differentiated, but there is still no anus.

(ii) *Larvæ with 11 pairs of cirri*.—This stage is represented by two specimens. The one studied alive was taken in the Red Sea (locality (i)). The shell-valves of this larva (fig. 5) are .82 mm. long, and .91 mm. broad, and the hinge-lines and the postero-lateral margins of the shell have acquired a brownish-yellow colour, which persists, and, indeed, usually increases in amount in older specimens. The eleventh pair of cirri has been recently formed. The anterior ocluser muscles have increased considerably in size, as compared with those of the previous specimens, and the posterior ocluser* is well formed. The two anterior dorsal liver-lobes are just beginning to grow out from the mid-gut, the intestine is now complete, and the anus is visible, opening into the mantle cavity about the middle of the length of the body-wall on the right side.

The first indication of the peduncle is seen as a hemispherical elevation, about 15μ high, on the ventral mantle-fold, near its posterior margin, behind and slightly to the right of the posterior ocluser. The peduncle of *Lingula* is evidently therefore not equivalent morphologically to that of *Terebratulina*, which is formed at a much earlier stage of development from the entire posterior region (the "third segment") of the larva.

On looking through a series of plankton-samples, obtained from a sea-water bath-tap on board ship by Dr NELSON ANNANDALE in 1901 in the Red Sea and Indian Ocean, I found, in the catch taken in the Strait of Bab-el-Mandeb on March 25, a larva similar in structure to that just described, but larger, its shell-valves being .92 mm. in length and .97 mm. in breadth.

(iii) *Larvæ with 12 pairs of cirri*.—This stage is represented by four specimens from the Red Sea (locality (i)). The dimensions of their shell-valves are :—

	Length.	Breadth.
<i>a</i> . .	1.0 mm.	1.0 mm.
<i>b</i> . .	1.06 „	1.07 „
<i>c</i> . .	1.1 „	1.05 „
<i>d</i> . .	1.1 „	1.07 „

It will be noted that, whereas in the examples previously described the shell-valves are broader than long, in the four now under consideration the length of the shell is equal to or rather greater than the breadth (fig. 3). The shell-valves have developed, in the neighbourhood of the hinge-line, a greenish colour which gradually fades away towards the lateral regions.

* Although the other muscles of the animal are well shown in the later stages, details of these muscles are not given, as I have nothing to add to Dr YATSU's account of them.

Each of the larvæ has 12 pairs of cirri, but in the smallest specimen (*a*) the most anterior cirrus on each side is a newly formed conical papilla about 40μ long. That the tips of the cirri can be protruded beyond the edges of the shell-valves was observed in life, and is further evidenced by two of the preserved specimens, in each of which one of the cirri has been "trapped" in the tightly closed valves, so that its tip is still projecting.

The posterior margin of the mantle, which even in the earliest larva examined was slightly pigmented, now exhibits clearly a yellowish-brown pigment, which extends forwards along the lateral mantle-margin.

Chætæ have been formed on each side in the postero-lateral region of the mantle. Two slender chætæ first appear close together. Along the middle and distal regions of each chæta are nodes, which in the middle portion of the chæta are at fairly regular intervals of about 8μ , but near the tip they are closer together (*cf.* fig. 7); in the basal part of the chæta they are less clearly marked. By the time these chætæ have increased in length to about $200\text{--}250\mu$, a few others of similar structure but shorter ($50\text{--}70\mu$ long) have been formed at intervals along the lateral and anterior margins of the mantle. About this time also gland-cells appear in the postero-lateral portions of the mantle in a zone a little removed from its margin; these gland-cells become much more abundant in the next stage (fig. 6), and finally extend all round the mantle, forming a glandular ridge. The area of the mantle median to this ridge is very thin and transparent. It may be noted here that the mantle is highly contractile, and, in a few of the preserved specimens, is withdrawn a considerable distance from the margins of the shell-valves. The radially arranged muscle-fibrils, by which the mantle is fixed to the shell, are well seen in most specimens.

The peduncle is bluntly conical in form and about $60\text{--}70\mu$ long. Its wall consists of a thick outer epithelium and an inner layer which is continuous with the coelomic epithelium (fig. 9). There is a central cavity which opens into the general body-cavity (fig. 6).

(iv) *Larvæ with 13 pairs of cirri.*—Six specimens at this stage of development were found along with the preceding examples in the Red Sea (locality (i)). The measurements of their shell-valves are—

	Length.	Breadth.
<i>a</i> . . .	1.17 mm.	1.15 mm.
<i>b</i> . . .	1.22 „	1.13 „
<i>c</i> . . .	1.28 „	1.14 „
<i>d</i> . . .	1.29 „	1.15 „
<i>e</i> . . .	1.29 „	1.17 „
<i>f</i> . . .	1.3 „	1.15 „

The maximum dorso-ventral diameter of each of the last four specimens is $.2$ mm.

The peduncle shows a marked increase in size during this stage; in the first two specimens (*a*, *b*) it is about 80μ long, but in the others it is $200\text{--}250\mu$ long,

and is bent upon itself near the middle of its length, so that the terminal part is dorsal and its tip directed to the left side.

The other organs are similar to those of the preceding stage, except that the two coelomoducts (nephridia) are now very clearly seen (fig. 10).

Three of the four larger larvæ of this group have been cut into serial sections, and a few notes on these may be given here (see figs. 8, 9, 10).

The shell was found to be in most parts about 20μ thick,* increasing to 30μ near the posterior margin, and to consist of a chitinous substance, a thin outer layer of which forms a not very clearly differentiated periostracum.

The statocysts (fig. 8) are closed sacs the external antero-posterior and transverse diameters of which are about $40-50\mu$, and the dorso-ventral diameter $10-15\mu$. Several minute statoliths in motion† were observed in each statocyst in the living specimens, but are not now visible. Each statocyst is situated in the dorsal body-wall at the point where the latter is joined by the lateral body-wall, and the appearances suggest that the statocyst was formed by an invagination of the epithelium in the lateral angle of contact of the two portions of the body-wall, but the statocyst now exhibits no trace of connection with the exterior.

The three ganglia of the central nervous system are situated in the body-wall; the ventral or sub-oesophageal (fig. 10) is much larger than the two lateral ganglia, which lie immediately in front of the anterior oclusors.

Muscle-fibres, almost longitudinal in direction, have appeared in the peduncle between the outer and inner cell-layers, but they are really formed in the latter.

The median tentacle bears long cilia at its tip on the ventral side. The tentacle is hollow, and the lumen,‡ which may not extend far into the distal half, contains cells and muscle fibres, the latter serving to bend or contract the tentacle. Surrounding the lumen in a zone of supporting substance of homogeneous nature, and around this is a layer, apparently nervous, which is in contact with the base of the sensory external epithelium.

Each cirrus is also hollow, and the lumen contains a bundle of longitudinal muscle-fibres which lie chiefly towards the medial side of the cirrus. The thick, external epithelium, which is ciliated on its median aspect, has very deeply staining nuclei. In the base of each cirrus there is homogeneous supporting substance, usually thinner or absent on the median aspect, which is continued into the two arms of the lophophore, where it forms, just proximal to the insertions of the cirri, a continuous curved band (fig. 9) supporting this basal portion of the arm-apparatus. The right and left bands are linked together by a small mass of the same kind of supporting substance situated in the mid-ventral wall of the lophophore near its

* The shells of these larvæ with 13 pairs of cirri are about twice as thick as those figured by Dr YATSU from his larvæ with 15 pairs of cirri. It may be noted that his larvæ, from the stage with 7-9 pairs of cirri onwards, were reared in captivity.

† Ciliated cells were not observed in the wall of the statocyst.

‡ The lumen opens posteriorly into the arm-sinus, which is connected with the general body-cavity.

posterior margin. The skeletal substance of the lophophore is therefore approximately U-shaped. This substance is, in these specimens, almost homogeneous and contains neither cells nor nuclei; it has evidently been secreted by one or both of the cell-layers in contact with it.

The mouth-cavity and oesophagus are lined with ciliated columnar cells, and the anterior and posterior walls of the stomach with high and narrow flagellated cells, those of the posterior portion of the stomach being especially striking. The intestine is apparently not ciliated. The digestive glands or "liver"-lobes are thick-walled diverticula of the mid-gut. There are two anterior dorsal diverticula—the smallest and last formed "liver"-lobes—situated in the dorsal and anterior part of the body-cavity; they are bounded laterally by the oclusors, and extend backwards as far as the gastro-parietal bands and forwards to the level of the anterior edge of the oclusors (fig. 8). These lobes unite ventrally and open into the anterior dorsal wall of the stomach by a very short median duct; dorsally the lobes are separated by the dorsal mesentery. The large posterior dorsal lobes of the digestive gland—one right and one left—open separately into the dorso-lateral portion of the stomach about the middle of its length (fig. 9). Each of these lobes presents an indication of subdivision into anterior and posterior portions. The ventral lobe of the "liver" is a large, A-shaped diverticulum (fig. 10)—that is, it is subdivided into right and left portions, which open by a common aperture at their anterior ends into the stomach near the middle of its ventral wall. The cells composing the "liver" are highly vacuolated—the vacuoles contained in life digestive secretion and oil globules,—cell-outlines are not distinguishable, and the nuclei are comparatively small. When the contents of the vacuoles have been removed, the walls of the "liver"-lobes have a spongy appearance, and embedded in them, here and there, are the unicellular algæ* on which the larva principally feeds.

The two coelomoducts (nephridia) could be clearly seen in the living larvæ, and are well seen in some of the whole mounts and in the sections (fig. 10). Their funnels, the apertures of which are directed postero-medially, lie in the coelom near the posterior end of the mid-gut, and are on the ileo-parietal bands. Each coelomoduct, the lumen of which is narrow, runs forwards in a curved course, and opens into the mantle-chamber on the antero-ventral wall of the body proper, immediately lateral to the anterior ocluser muscle—that is, ventral and a little postero-lateral to the mouth.

(v) *Larvæ with 14 or 15 pairs of cirri*.—Four large specimens were found in the Red Sea, two of them on June 21 at locality (i), the others on October 22 at locality (iii). The measurements of their shell-valves are—

		Length.	Breadth.
a, October 22, 1914	.	1.47 mm.	1.22 mm.
b, June 21, 1914	.	1.48 "	1.22 "
c, October 22, 1914	.	1.52 "	1.22 "
d, June 21, 1914	.	1.6 "	1.37 "

* A Radiolarian was also noticed in the gut.

Growth in length of the shell-valves is evidently taking place at this stage much more rapidly than growth in width, as the later growth-lines show (fig. 4). The shell has now become elliptical, the longer axis being antero-posterior. In specimens *a* and *b* there are 14 pairs of cirri; in *c* and *d* the number of pairs is apparently 15, but as the cirri are closely packed together it is difficult to be certain of their number.

Additional chætæ have been developed in the postero-lateral region of the mantle, where there is now a group of about six or eight long chætæ on each side, among which the two original ones may generally be distinguished by their slightly greater length and thickness (fig. 6). Other shorter chætæ have been added at intervals round the lateral and anterior margins of the mantle.

The posterior occlusor is now a round or oval cylinder of muscle about 80–100 μ in diameter. The peduncle is from .4 to .8 mm. in length,* and is bent into one or two loops, its terminal part lying dorsal to the proximal part, and its tip pointing to the left (fig. 6). The terminal portion of the peduncle is dilated, and the epithelium covering this region is much higher than elsewhere, but it has not yet proceeded to form the secretion which later envelops it. The peduncle, which is colourless, is in each specimen enclosed within the shell-valves, no part of it being extended.

The median sensory tentacle does not exhibit the least sign of reduction; it is still large, about 160 μ long, and is evidently fully functional.

These specimens are the largest and latest free-swimming stages recorded for any species of *Lingula* (*s. lat.*). Probably these larvæ would soon have settled down, the peduncle of each would have been extended beyond the valves, and the high epithelium of its terminal portion would have produced secretion by means of which the larva would have fixed itself to the substratum.

A note of the colours exhibited by the living larvæ may be given here. The shell-valves, even of the largest larvæ, are transparent, there being no calcareous matter present. As already mentioned, the posterior and neighbouring lateral margins of the valves are yellowish brown, and in these regions the zone just within the margin is a bright green colour. The mantle-margin is usually brownish, especially posteriorly. The basal half of the tentacle, particularly on the dorsal side, and the distal portions of the cirri, are yellowish brown, and there is a patch or spot of deeper tone at the tip of most of the older cirri, and a similar spot about the middle of the dorsal surface of the tentacle. There is yellow pigment on each side of the mouth at its postero-lateral margins. The "liver"-lobes are lemon-yellow, and near their periphery a small amount of brown pigment is present.

* The largest specimen seems to be abnormal in this respect, for the peduncle is comparatively short—about .2 mm. in length,—but it is not possible to state its length exactly, owing to its being much foreshortened, as seen in the preserved specimen.

COMPARISON OF THE LARVÆ WITH THOSE PREVIOUSLY RECORDED.

The larvæ described in the foregoing account fall into a single series, and evidently all belong to one species. On comparing them with those described by Dr YATSU, there can, I think, be no doubt they belong to the same species—*Lingula anatina* Bruguière,—which is, so far as I am aware, the only species recorded from the Indian Ocean. In structure and colours my larvæ agree closely with Dr YATSU's, and special points of agreement are: the hinge-line is practically the same length in both series of larvæ, and the chætæ evidently arise in the same manner, for it is clear from Dr YATSU's figure (*e.g.* fig. 86) that in his larvæ, as in mine, the two chætæ first formed in the postero-lateral region remain for a considerable time distinguishable from those formed later.

Captain SEWELL concluded that his larvæ also were those of *L. anatina*.

There are certain differences between my larvæ and those of Dr YATSU and Captain SEWELL which may be now considered.

(a) *Size*.—The following table summarises the average dimensions of the shell-valves of the larvæ of different stages :—

No. of Pairs of Cirri present.	YATSU.		SEWELL.		ASHWORTH.	
	Length.	Breadth.	Length.	Breadth.	Length.	Breadth.
5	·31	× ·39 mm.				
6	·44	× ·41 „				
7-8	·66	× ·61 „			·52	× ·62 mm.
			...			
			(December Series.)			
9		...	·65	× ·66 mm.		
10		...	·82	× ·77 „	·76	× ·81 „
11		...	·89	× ·80 „	·87	× ·94 „
12		...		...	1·06	× 1·05 „
13		...		...	1·26	× 1·15 „
			(February.)			
14		...	1·11	× 1·11 mm.	1·48	× 1·22 „
15	·8	× ·64 mm.		...	{ 1·52	× 1·22 „
					{ 1·6	× 1·37 „

Dr YATSU's larvæ with 7 or 8 pairs of cirri were rather larger than mine, but his later stages were much smaller—compare them when they have 15 pairs of cirri. This disparity is no doubt due to the fact that Dr YATSU's larvæ, from those with 8 or 9 pairs of cirri onwards, were kept in aquaria, and the growth of the shell was retarded, for it may be noted that the shell-valves of his specimens were not only smaller but much thinner (see p. 51 and footnote). Captain SEWELL's larva with 14 pairs of cirri is considerably smaller than mine, but as he suggests that the conditions at the time of the year when it was taken were unfavourable, the difference in size may be due to this cause.

(b) *Change in the Shape of the Shell*.—The table serves to show that the change in the shape of the shell-valves—that is, when they become for the first time longer

than broad—took place at different stages in each of the series of larvæ under consideration. In Dr YATSU's this change occurred when 7 or 8 pairs of cirri were present, in Captain SEWELL's specimens collected in December the change took place when 9 pairs of cirri were fully formed, and in my larvæ when 12 pairs of cirri were present. Captain SEWELL's single specimen taken in February had a shell as long as broad; he attributes the delay in change of the shape of the shell* to the less favourable time of the year when development was taking place.

(c) *Chætæ*.—Chætæ appeared in Dr YATSU's larvæ at an earlier stage than in mine, but in both series the time of appearance of the chætæ coincided with the change in shape of the shell-valves.

(d) *Peduncle*.—In Dr YATSU's larvæ the peduncle appeared when 6 pairs of cirri were present, and was protruded by the time 10 pairs of cirri had been formed, at which stage his larvæ, kept in aquaria, became fixed. Perhaps the artificial conditions brought about precocious fixation. In Captain SEWELL's larvæ the peduncle began to develop in the stage presenting 9 pairs of cirri, but there was no sign of its protrusion in his specimens with 11 pairs of cirri. In my larvæ the first trace of peduncle did not appear until 11 pairs of cirri were present, and the peduncle was entirely internal in the largest larvæ, which had 15 pairs of cirri and were still free-swimming.

(e) *Tentacle*.—In my largest larvæ, with 14 or 15 pairs of cirri, the median sensory tentacle was not in the least degree reduced, but was fully functional, whereas in Dr YATSU's examples with 15 pairs of cirri—the specimens being then attached to the bottom of the aquaria—the tentacle was either absent or reduced to a small papilla. Dr YATSU regards the tentacle as a larval organ, and therefore considers its disappearance in his fixed specimens as a natural consequence. There is, however, the possibility that the conditions of captivity had determined the reduction and eventual loss of this sense-organ in his larvæ. A similar tentacle is present in *Glottidia*; and in BROOKS's figure (fig. 7) of a young specimen, with 16 pairs of cirri, soon after it had become sedentary, the tentacle is shown as long as the neighbouring cirri, and BROOKS states definitely (p. 73) that it is persistent.

Most of the differences between the various series of larvæ discussed above, particularly in reference to the size of the shell-valves, the size and protrusion of the peduncle, and perhaps the persistence or loss of the tentacle, are doubtless dependent almost entirely on the environmental conditions. Variations in one or more of these characters may be expected in larvæ of the same species obtained in widely separated areas and under diverse conditions. There are, however, certain features which appear to be more constant for the species, at any rate they present a fairly close agreement in Dr YATSU's larvæ and mine †—namely, the length of the hinge-line and

* The peduncle of this specimen was also in a backward state, being "still only a small rudiment."

† In Captain SEWELL's larvæ there was apparently a rather greater range of variation in the length of the hinge, but its average length in his twelve larvæ was 3 mm., practically the same as in Dr YATSU's and mine.

the antero-posterior diameters of the valves of the protegulum,* and probably also the form of the chaetæ. These features may therefore be found useful in the determination of the species of larvæ, but a definite decision as to their taxonomic value can only be reached after they have been examined in further series of specimens.

Judging from the large size attained by the oldest examples, the larvæ found in the southern portion of the Red Sea developed under very suitable conditions. It will be observed that these larvæ form a regular series, there being no aberrant members, and they probably afford a fairly reliable criterion of the normal course of development in a favourable environment.

BREEDING SEASONS.

Dr YATSU states that the breeding season at Misaki is very short, and is certainly restricted to a month and a half of the summer—from the middle of July to the end of August. He estimates that the period which elapses from the onset of development to the stage with 15 pairs of cirri is about six weeks. Assuming that my larvæ had developed at about the same rate, the oldest specimen, with 15 pairs of cirri, taken on June 21, 1914, in the southern portion of the Red Sea, would be one of the products of a spawning which had taken place in the first half of May. Spawning evidently continued until, or was resumed about, the end of May, for a much younger larva, only half as long as the preceding, was taken at the same time and place. The finding of two large larvæ, with 14 and 15 pairs of cirri respectively, in the southern portion of the Red Sea on October 22, is evidence that a spawning occurred in the first half of September. The specimen in Dr ANNANDALE'S material was taken on March 25, 1901, in the Strait of Bab-el-Mandeb, and probably had developed from an egg fertilised about a month previously. The evidence available in regard to the southern end of the Red Sea indicates that there is a succession of spawnings extending at least over the period from the beginning of March to the early part of September.

Captain SEWELL records the occurrence of larvæ during the winter months, December and February, in the plankton off the south coast of Burma. I found one young larva, which was probably from two to three weeks old, in the Indian Ocean, about 3° N. lat., and 80° E. long., on October 14, 1914.

COMPARISON OF THE LARVÆ OF *LINGULA ANATINA* WITH BROOKS'S LARVÆ OF *GLOTTIDIA AUDEBARTI*.

As BROOKS'S memoir (1879) on the development of *Glottidia* is not easily accessible, a few notes on his specimens are given here, and their characters compared with those of the available examples of *Lingula anatina*.

* The primary shell is laid down while the larva is enveloped by the egg-membrane, and hence the protegula and the hinge-line are determined under relatively uniform conditions; later the larva is subject to more diverse conditions, which cannot but react upon such characters as the secondary shell and the peduncle.

The three free-swimming larvæ figured by BROOKS have shell-valves with the following dimensions :—

No. of Pairs of Cirri.	Shell-Valves.	
	Length.	Breadth.
5- 6	·23 mm.	·27 mm.
7- 8	·29 „	·29 „
9-10	·4 „	·37 „

These larvæ, and especially the two last, are much smaller than those of *Lingula anatina* with the same number of cirri. The distance between the teeth at the ends of the hinge-line on the ventral valve in BROOKS's larvæ is ·15-·16 mm., as compared with about ·3 mm. in *L. anatina*; and the antero-posterior length of the protegulum of the dorsal valve is about ·065 mm. in BROOKS's larvæ (figs. 1 and 3), and ·12 mm. in *L. anatina*.

Chætæ are formed in the larvæ of *Glottidia* when about 9 pairs of cirri are present, and are shown (BROOKS's fig. 3) all of the same size and sparsely scattered round the margin; there is apparently not a larger first-formed pair on each side as in *L. anatina* (see p. 50). It will be noticed that the chætæ appear about the same time as the change in the shape of the shell-valves takes place, as was also the case in *L. anatina*.

The posterior occlusor and the peduncle are formed when 7 pairs of cirri are present, and by the time there are 10 pairs of cirri the peduncle has become long and looped, and BROOKS expressed the opinion that the larvæ became sedentary soon after this stage, but the change was not actually observed, as it was found that "the larvæ could not be made to thrive in confinement."

The youngest sedentary example of *Glottidia* found has 16 pairs of cirri. The shell-valves of this specimen are about 2 mm. long and 1 mm. broad, and the peduncle—now fully protruded—about 5-6 mm. long. In the dorsal and in the ventral mantle-lobe there are four pigment-spots near the anterior margin; there are no pigment-spots in my larvæ of *Lingula* 1·52 and 1·6 mm. long respectively, nor do they appear to have been present in Dr YATSU's specimens.

The most noticeable differential characters of BROOKS' specimens of *Glottidia* are: in the free-swimming stages, the small size of the shell-valves, the short hinge-line and consequently the small protegulum; in the sedentary specimen, the narrow shell-valves* and the presence of pigment-spots near the anterior mantle-margin.

BROOKS's larvæ of *Glottidia* were obtained in Chesapeake Bay, and as young stages were found in the middle of July, while only older larvæ were taken in the middle of August, the breeding season was probably short, as was also found by Dr YATSU for *Lingula* at Misaki, which is in nearly the same latitude as Chesapeake Bay.

* In this connection it may be remarked that full-grown examples of *Glottidia audebarti* do not attain so large a size as those of *Lingula anatina*, and the shell-valves of the former are narrower in proportion to their length.

THE LARVÆ OF PELAGODISCUS (DISCINISCA).

PREVIOUS RECORDS OF THE LARVÆ OF DISCINIDÆ.

(a) *Larvæ of Pelagodiscus (Discinisca) atlanticus* (King).—FRITZ MÜLLER (1860, 1861) was the first to describe a larva of an ecardinate Brachiopod. He recognised that his larvæ were those of some Brachiopod, but in his published accounts did not refer them to any genus, though he evidently not long afterwards* reached the conclusion that they belonged to the genus *Discina*.† He probably saw about a dozen living larvæ, which he collected in the years 1859 and 1860 near Desterro on the southern portion of the coast-line of Brazil.

The only other observer who has hitherto seen a living larva is Dr YATSU (1902, p. 105) who found, in the plankton near Misaki (Japan), a specimen which is probably referable to the species *P. atlanticus*.

Professor BLOCHMANN (1898) studied ten preserved examples taken in the plankton off the island of Bintang, about 45 miles south-east of Singapore.

(b) *Larvæ of other Discinidæ*.—MÜLLER obtained another larval form of a species of *Discina*, which he stated, in a letter to Professor MORSE,* belonged to the species *D. radiata* Dunker, but I am unable to find any further reference to this larva, no description of which seems to have been published.

Professor SIMROTH (1897, pp. 3-6) has described two larvæ obtained by the Plankton Expedition. The smaller one, from Palmas roadstead, has a transverse diameter of .22 mm., and only 3 pairs of cirri. It is further remarkable for possessing on each side four very long chætæ. The larger larva, taken in lat. 5° 9' N., and long. 20° 3' W., at a depth of 1000-1200 mètres, has a transverse diameter of .42 mm. This larva has 4 pairs of cirri, which are much more slender and elongate than those of *P. atlanticus*, and the median tentacle is also elongate and terminates in a bulbous dilatation. There are only two chætæ on each side, which appear to be equal in length and simple. Both these larvæ are referred by Professor SIMROTH to the genus *Discina*.

EICHLER (1911) has given a short account of two larvæ obtained by the German South Polar Expedition near the winter station of the *Gauss* (lat. 66° S., long. 90° E.), from a depth of 3000 mètres. The specimens were .787 and .825 mm. respectively in transverse diameter, and had 4 pairs of slender cirri of unusual length. On each side there were four stronger chætæ, all of similar form and

* Professor MORSE (1873, pp. 356, 357) states that he received "a letter from Herr MÜLLER, accompanied with a sketch of another larval form of *Discina*, in which he describes features similar to those above mentioned [referring to his abstract of the account of MÜLLER's larvæ from Desterro], and states that the species has been defined by Professor DUNKER as *D. radiata*." By the courtesy of Mr E. A. SMITH I have been able to see DUNKER's description of *D. radiata* (*Malak. Blätt.*, vol. viii, p. 39, 1861): there is no reference to the larva.

† The genus *Discina* was subdivided by DALL in 1871 into *Discina* (*sensu stricto*) and *Discinisca*, and the latter was again divided by DALL in 1908 into *Discinisca* (*s. str.*) and *Pelagodiscus*. *Discina atlantica* King falls into the last-named section, and its correct designation is therefore *Pelagodiscus atlanticus* (King).

apparently simple, *i.e.* not spinulose, and a series of finer chætæ on the lateral margin of the mantle. EICHLER and BLOCHMANN consider that these larvæ probably belong to *Pelagodiscus* (*Discinisca*) *atlanticus*; but there is no justification for referring them to this species, from which they differ in the following characters: their much greater size, the form of the median tentacle, their cirri (which are about three to four times as long as those of *P. atlanticus*), and in their possession of only four principal chætæ, the longest of which is not specially stout. These larvæ differ so strikingly from those already referred on good grounds to *P. atlanticus* that they cannot be regarded as belonging to the same species; they may be larvæ of some larger species of *Discinisca*.

THE LARVÆ OF PELAGODISCUS (*DISCINISCA*) ATLANTICUS.

Six free-swimming larvæ were taken on October 16, 1914, in the Indian Ocean a few miles west of Cape Comorin, where the chart shows depths of about 40 fathoms.

Adult specimens of *P. atlanticus* have been found almost entirely in deep water; there are records from 200 and 690 fathoms, but with these exceptions specimens have been found only at depths greater than 1000 fathoms, and there are four records from more than 2000 fathoms, the deepest being 2425 fathoms. The occurrence of the larvæ of *Pelagodiscus* off Cape Comorin in shallow water was therefore rather unexpected. The fact that half a dozen larvæ were obtained together indicates the probable close proximity of the parent forms. There is, however, the possibility that the adults lived in the deep water to the west, for the depth increases rapidly in that direction, and there was deep water—700–800 fathoms—only about thirty miles away. It is known that the larvæ may remain free-swimming for five or six days,* a period which would have been sufficient for their transportation by the strong currents from the area of deep water to the locality where they were found. Although the conditions suggest that the adults of *P. atlanticus* occur in shallow water near Cape Comorin, a definite conclusion cannot be reached on the evidence available.

I have recently looked over charts† of the other areas from which larvæ of *Pelagodiscus* have been recorded. Around Desterro, where MÜLLER found his larvæ, the sea is shallow, the nearest water of 100 fathoms depth being some sixty miles eastwards. Off Bintang, where Professor BLOCHMANN's ten larvæ were taken, the water is very shallow (0–24 fathoms), the nearest water of 100 fathoms depth being about four hundred miles away. At Misaki, where Dr YATSU took a single larva, there is deep water close inshore. It is evident from a consideration

* MÜLLER (1861, p. 54) observes, regarding his larvæ in aquaria: "Die Dauer dieses Schwärmstadiums überstieg bei den eingefangenen Larven nie 5-6 Tage, meist schon früher setzten sie sich fest, am Boden oder an den Seiten des Glases." SCHUCHERT (*Bull. Geol. Soc. Amer.*, vol. xxii, 1911, p. 272), however, states that the larvæ "are known to live in the free and floating condition for nearly a month," but there is no evidence in support of this statement, which is erroneous.

† I am indebted to Dr W. S. BRUCE for giving me access to the charts in the Scottish Oceanographical Laboratory.

of the conditions in the areas where the larvæ recorded by MÜLLER and BLOCHMANN were taken that the adults of *P. atlanticus* are not confined to deep water, and the occurrence of the larvæ in shallow water near Cape Comorin, while not conclusive, lends support to this view.

Description of the Larvæ (Plate V).

The six larvæ agree closely in size and structure, and are evidently all about the same stage of development.

The shell-valves (fig. 11), which are unequal, are free from each other all round their margins, there being no hinge; they are connected only by the muscles—especially the oclusors, and the body-wall. The dorsal valve, which is almost like a watch-glass in form, is sub-circular and varies in the different specimens from .39–.43 mm. in length, and .43–.47 mm. in breadth. The almost flat ventral valve, which has a peduncular sinus in the posterior middle line, is .32–.34 mm. long, and .39–.42 mm. wide. The maximum dorso-ventral diameter of each of the three larvæ in which it was measured is .075 mm. These larvæ are about the same size as those described by Professor BLOCHMANN and that by Dr YATSU, and slightly larger than MÜLLER's original examples. Both valves are chitinous and transparent, and exhibit no trace of calcareous substance. The edge of the dorsal valve, and to a less extent that of the ventral valve, are yellowish brown in colour. The shell-valves vary in thickness in different portions from about 3 to 8 μ . The chitinous shell, which cuts easily in paraffin, is covered on its external surface by a definite, though very thin periostracum, which is continued over the edges on to the inner face of each valve, where, overlying the thin margin of the mantle, it extends inwards until it reaches the thickened zone of the mantle by which it is evidently formed. In surface view the periostracum presents a shagreened appearance.

The mantle is for the most part colourless, but in its postero-lateral margins exhibits some yellowish-brown pigment, and along the margin of the peduncular notch bears darker brown pigment-granules. The mantle is very thin over the greater part of its extent, but presents a thickened zone in its lateral and anterior portions in both valves, but especially in the dorsal valve (fig. 17). The posterior mantle-margin is thin in the dorsal valve, and in the ventral one forms a narrow strip posterior to the peduncle. In the thin portions of the dorsal and ventral mantle-folds, the outer surface of which is, of course, applied to the shell, there are numerous gland-cells containing large granules; these cells no doubt secrete the shell. In the thickened zone of the mantle there are, besides gland-cells, more numerous epithelial cells and some muscle-fibres; the chaetæ are implanted in this region, which, as already stated, secretes the periostracum.

There are five pairs of principal chaetæ, as described by MÜLLER (1860). Additional details regarding them may be given here. The two anterior chaetæ of each side are slender and flexible, and are about .15–.16 mm. long. Each has a simple

joint situated a short distance proximal to the middle of its length, and the flattened and tapering distal portion exhibits faint indications of several joints, and bears along one margin minute spinules, which, however, do not extend to the tip of the chæta (fig. 13). When at rest these chætæ usually point antero-medially, but in preserved specimens they may be found directed antero-laterally owing to the contraction of the museles attached to their bases. The third chæta is usually gently curved, about .09 mm. long, and is directed postero-laterally. It bears on its anterior edge minute, regularly arranged, pointed processes, which begin a little proximal to the middle of the length of the chæta, but do not extend to its tip (fig. 14). The fourth chæta is the largest, being .3-.33 mm. long, and much thicker than the others. It issues between the shell-valves postero-laterally and then usually curves towards the middle line, as shown on the right side of fig. 11, but it may be turned so as to point outwards, as on the left of fig. 11. Its proximal portion—about one-fifth—which is almost uniform in diameter, merges into a dilated region where the chæta issues between the two shell-valves; distal to this the chæta tapers gradually to its tip. The greater part of the tapering portion is beset, except on its medial side, with numerous pointed teeth or thorns, the tips of which are directed postero-laterally (fig. 15). The thorns do not extend quite to the tip of the chæta; a terminal portion about 15μ long is without them and is very fragile. The four pairs of chætæ described above arise from the ventral mantle-fold. The fifth chæta on each side, which arises from the dorsal mantle-fold, is about .18-.2 mm. long. It is slender and strongly curved so that its tip points postero-medially, and it bears, on its distal half, minute spinules similar to, but smaller than, those of the fourth chæta. Museles are attached to the bases of each of these five chætæ.

There is also on each side a series of about thirty chætæ, all of similar form, regularly arranged in close order in the thickened zone of the dorsal mantle-fold, and extending from the region of the fourth principal chæta forwards almost to the middle line. These chætæ are almost uniform in diameter along the greater part of their length, but taper rapidly at their tips. They exhibit nodes at intervals, and are flexible; they are usually directed postero-laterally, and their free ends are bent under the edge of the ventral valve. Only the two most anterior and the most posterior of these chætæ (CH. S.) are shown on the right of fig. 11.

On each side are two or three thicker chætæ situated in the ventral mantle-fold, about midway between the second and third principal chætæ, and directed almost laterally (fig. 11, right side). Each of these bears longitudinal striations and is subdivided by nodes so that it resembles a bamboo (fig. 16).

The peduncle, as seen in the living or stained specimen (fig. 11), is an oval mass, the transverse and antero-posterior diameters of which are, on an average, about .13 and .04 mm. respectively. In vertical section (fig. 17) the peduncle appears as an elevation, triangular in section, of the inner wall of the ventral mantle-fold close to

its posterior margin, so that in its origin it is similar to that of *Lingula* (see p. 49). The broad base of the elevation is ventral, the posterior or dorsal side of the ridge lies parallel and close to the dorsal mantle-fold,* and the anterior side is almost parallel to the posterior wall of the body proper. The epithelium covering the peduncle is continuous with, but much thicker than, the inner epithelium of the ventral mantle, which unites with the epithelium of the body-wall proper just anterior to the front margin of the peduncle. The central portion of the peduncle consists of strong curved muscle-fibres, which have a general ventro-dorsal direction. A narrow transverse cavity is present in the posterior portion of the peduncle, but this does not appear to have a definite epithelial lining, nor is there any visible connection in the preserved specimens between this cavity and the body-cavity, though there is probably a connection in life, as in the case of *Lingula* (p. 50 and fig. 6). The narrow strip of mantle immediately posterior to the peduncle is strongly pigmented, and the pigment extends forwards right and left into the epithelium which covers the sides of the peduncle. The dorsal and anterior faces of the peduncle are almost completely covered with a thin film of periostracum. The peduncle is in condition to be extended ready for fixation; the small lip at the posterior margin of the ventral valve, which consists only of periostracum, would be bent ventrally, and the neighbouring region of the ventral valve would yield to some extent so as to permit the exit of the peduncle between the shell-valves. During extension the peduncle would be so bent as to bring its flat, previously dorsal, surface into contact with the object to which fixation was about to take place, and the granular cells forming the thick epithelium of that face of the peduncle would secrete the necessary cementing substance.

The median tentacle is an elevation on the epistome about $30-40\mu$ in height and 50μ in width. Its apex is traversed by a shallow median groove, the cell of which are pigmented. The apical portion of the tentacle is solid, but the basal half contains a narrow axial lumen, which opens proximally into the arm-sinus. The lumen is lined by cells and contains longitudinal muscle-fibrils by means of which the tentacle can be contracted or bent laterally or ventrally towards the mouth. Supporting tissue, like that found in the tentacle of *Lingula* (see p. 51), is not present, but there is a nervous layer between the lumen and the epidermis. The tentacle is ciliated along two tracts (indicated by the darker areas in fig. 11), one on each side, near its base.

The discoidal lophophore bears the mouth near the middle of its ventral surface, and on each of its lateral margins there are, in all the specimens except one, four approximately equal cirri arranged as shown in fig. 11. In one of the larvæ (not the smallest) there are four cirri, all of normal size, on the right side, but on the left there are only three, the fourth or most anterior cirrus being absent. The cirri

* The peduncle is not in any way connected with the dorsal valve; its posterior surface may touch the dorsal mantle-fold, but remains quite independent of it.

are hollow, and the comparatively large cavity, which opens into the arm-sinus, is lined by an epithelium and contains longitudinal muscle-bands. The cells on the medial face of each cirrus bear long cilia. As in *Lingula*, the deeply staining epithelium of the cirri is thrown into annular folds by contraction of the museles. Supporting substance is not recognisable in sections of the cirri, but is present in each half of the lophophore as a narrow band lateral to the arm-sinus, and extending along the region of attachment of the cirri. The greater part of each cirrus, the distal region of the tentacle and the ciliated tracts, right and left, in its basal portion were yellow in life. There was also a considerable amount of yellow pigment in the lip which overhangs the mouth in front, and a narrow transverse band of brownish pigment in the ventral body-wall immediately anterior to the sub-œsophageal ganglion.

There is a deep depression on the ventral side between the posterior margin of the lophophore and the anterior edge of the wall of the body proper (fig. 17). In this depression, and situated on the anterior surface of the wall of the body proper, just ventral to the œsophagus, is the large ventral nerve-ganglion. The two lateral ganglia, which are also large, are situated in the body-wall in front of the anterior margins of the oclusors.*

The outline of the wall of the body proper is almost semicircular or bluntly conical, its form and height depending on the condition of expansion or contraction of the animal. In the lateral wall of the body proper, rather nearer the dorsal than the ventral surface, is on each side a large black, or brownish-black, oval pigment-spot or "eye," about 20μ long. Similar pigment-spots were present in the larvæ examined by FRITZ MÜLLER, but not in those described by Drs BLOCHMANN and YATSU.

The epidermis of the body-wall in the region of the "eye," especially ventral and posterior to it, is higher than elsewhere, and forms a regular columnar epithelium. This elevation, which is readily seen in most specimens mounted whole, probably represents a sensory area.

The "eye" is like a shallow cup in shape (fig. 18), and consists of masses of brown pigment-spherules deposited in the distal ends of several of the epithelial cells. Immediately below the epithelium of this region of the body-wall is a nervous tract extending backwards from the lateral ganglion, which supplies the columnar epithelium described above, the "eye," and the statocyst.

In the dorsal body-wall on each side is a large statocyst situated immediately posterior and slightly lateral to the dorsal margin of the massive anterior oclusor muscle (fig. 12). The maximum internal diameter of the statocyst is about 25μ ; the external diameters are: antero-posterior, $30-40\mu$; transverse, $25-30\mu$; dorso-ventral, $10-15\mu$. In surface view the statocyst is ovoid, and the narrower end,

* That is, the anterior oclusors; there are no posterior oclusors at this stage. Professor BLOCHMANN has given an account of the muscles of the larva, to which I have nothing special to add.

which is directed anteriorly, lies near the lateralis muscle. Several minute statoliths were present in life, forming a small mass in the centre of the statocyst. The wall of the statocyst consists of two layers: an epithelium with large nuclei similar to the epithelium of the neighbouring region of the mantle, and a thin enveloping layer of coelomic epithelium (fig. 18). The statocyst is in contact with the body-wall at the angle of union of the latter with the dorsal mantle, and in this angle is a distinct depression in the external epithelium suggesting that the statocyst had been formed by invagination at that point. Professor BLOCHMANN holds that the organs interpreted as statocysts are really the funnels of nephridia,* and describes and figures an "Ausführungsgang." There can, however, be no doubt that the organs in question are statocysts, and they are closed sacs. Dr YATSU (1905, p. 563) states that the statocysts "must become smaller at the time of attachment" of the larva, but his fig. 2 from a young attached *Discinisca larvis* shows a statocyst considerably larger than that of a free-swimming *Pelagodiscus atlanticus*.†

The mouth is situated immediately behind the epistome by which it is overhung; its cavity is lined by ciliated cells. The œsophagus, which has a high columnar ciliated epithelium, passes at first dorsally and, after a short course, turns through a right angle to run posteriorly. It opens, at the level of the body-wall, into the mid-gut by a somewhat constricted aperture. The mid-gut is widest posteriorly; it represents the stomach and the digestive gland or "liver," the lobes of the latter not having yet been formed. The cells of the wall of the mid-gut are, however, sharply differentiated into two kinds: high epithelial flagellated cells which will form the wall of the stomach, and vacuolated cells which will be included in the future lobes of the "liver" (fig. 17). The high epithelium characteristic of the stomach is present in (1) the anterior wall of the mid-gut, but only for a short distance around the point of entrance of the œsophagus; (2) in the middle and posterior portions of the ventral wall; and (3) in the ventral half of the posterior wall of the mid-gut. The remainder of the mid-gut, comprising the entire dorsal and lateral walls, the dorsal half of the posterior wall, and the anterior portion of the ventral wall, will form the "liver"-lobes. The epithelium of the stomach, especially that of the posterior ventral region, is remarkable for the height and slenderness of its cells, which are 11–15 μ long, but not more than 1 μ wide at their distal ends. The elongate, deeply staining nuclei are situated in the proximal portions of the cells. Each cell bears only a single flagellum about 8–12 μ long, which arises from a well-marked basal granule in the distal region of the cell (fig. 19). Many of the "liver"-cells are highly vacuolated; the remaining cells are filled with spherules or less regular masses of secretion. The nuclei are at the bases of the cells, and cell-outlines cannot be distinguished. The "liver"-tissue is similar in structure to

* See also footnote, p. 48.

† In *Lingula* the statocysts do not diminish in size when the animal becomes sedentary, as may be seen from the figure of a statocyst of a sedentary example with shell 6.5 mm. long given by Dr YATSU (1902a, fig. 22). This statocyst is about three times as large as those of the larvæ described on p. 51.

that of *Lingula*, but the contents of the cells, as seen in life, are not so refringent. The intestine, which is not ciliated, issues from the ventral wall of the mid-gut near the middle line and a little anterior to its hinder margin (fig. 11). It runs towards the right and is at first narrow, but becomes wider as it enters the postero-lateral corner of the body-cavity, where it is dilated into a sub-spherical sac from which the narrow terminal portion runs anteriorly and slightly laterally to open on the body-wall ventral to the pigment-spot and near the postero-lateral margin of the right anterior oclusor. The mid-gut is pale yellow in colour, and scattered through the "liver"-cells there is a considerable amount of brownish pigment.

The larva feeds on unicellular algæ; spherical algæ and a few diatoms are present in the gut.

The cœlom is not spacious; there are, however, obvious portions of the cœlom in the postero-lateral regions of the body and a connecting transverse cavity posterior to the mid-gut. Unfortunately, I have no observations on the cœlomic fluid or its contents in life.

All the specimens possess a pair of cœlomoduets (nephridia), which have not hitherto been observed in the free-swimming larvæ of any Discinid. The funnel of each cœlomoduct is situated on the ileo-parietal band about the level of the posterior margin of the mid-gut; its opening is directed posteriorly and rather towards the middle line (fig. 11). The funnel leads into a slender tube which can be traced forwards a little more than half way along the lateral margin of the oclusor muscle to its opening into the mantle-chamber. The total length of the cœlomoduct is about 70–90 μ . The funnel appears in section as a double series of cells with deeply staining nuclei, representing the two lips, between which is a narrow lumen. The dorsal lip is slightly longer than the ventral. The rest of the duct is lined with a flat epithelium and ensheathed with a very thin cœlomic epithelium. The lumen of this portion is widest about the middle of its length, where it may attain a diameter of 5 μ , but is usually much narrower (2–3 μ).

The larvæ described above correspond exactly with those studied by FRITZ MÜLLER, and they agree with those described by Drs BLOCHMANN and YATSU except that their specimens had no pigment-spots ("eye-spots"). This difference, in view of the close agreement in other respects, should probably not be considered as significant; it may be merely a local variation.

Professor BLOCHMANN has adduced cogent evidence for regarding the larvæ described by MÜLLER and himself as belonging to *Pelagodiscus* (*Discinisca*) *atlanticus*. The identity of my larvæ with those of MÜLLER and BLOCHMANN seems so clear that they may safely be referred to the same widely distributed species, the range of which is now extended into the Indian Ocean. There is, so far as I am aware, no record of adults of *P. atlanticus* from the Indian Ocean, and the nearest record of the species is that of Professor BLOCHMANN, whose larvæ were taken off the island of Bintang.

It is interesting to notice that all the known larvæ of *Pelagodiscus atlanticus*—about thirty altogether—have 4 pairs of approximately equal cirri.* MÜLLER was able to keep his larvæ under observation in aquaria, and it is evident from his accounts that they became fixed at the stage with 4 pairs of cirri. Dr YATSU (1905) found a young attached example of a related species, *Discinisca lavis*, which had 6 pairs of cirri, so that in this species also attachment of the larva occurs at or not long after the stage with 4 pairs of cirri. These facts account for the absence of free-swimming stages with more than 4 pairs of cirri, but there is no satisfactory explanation why earlier larvæ have not been found. MÜLLER (1860, p. 79) suggested that the younger stages may be retained in the shell of the parent, but I am not aware of any evidence in support of this view. It may be that the younger stages live on the sea-bottom and hence have hitherto escaped capture; all the larvæ of *Pelagodiscus* recorded have been taken at or near the surface.

Breeding Season.—Few data are available on this point. Professor BLOCHMANN's specimens were collected off Bintang on July 3, 1899, and mine were taken off Cape Comorin on October 16, 1914. Dr YATSU does not state when he found his specimen, but, as it occurred among the larvæ of *Lingula* at Misaki, it must have been in the period from the latter part of July to the middle of September.

MÜLLER states that at Desterro, Brazil, the larvæ occurred in late summer, from February to April, a season which corresponds approximately with the period in which the larvæ have been found in the northern hemisphere.

LIST OF LITERATURE.

- BLOCHMANN, F., "Die Larve von *Discinisca*," *Zool. Jahrb., Abt. Anat.*, Bd. xi, pp. 417-426, Taf. 31, 1898.
 BLOCHMANN, F., "Unters. über den Bau der Brachiopoden," ii. Jena, 1900.
 BROOKS, W. K., "The Development of *Lingula*," *Chesapeake Zool. Lab. Sc. Results of 1878*, pp. 35-112, pls. 1-6. Baltimore, 1879.
 EICHLER, P., "Die Brachiopoden der deutschen Südpolar-Exped.," *D. Südp.-Exped.*, Bd. xii, *Zool.*, iv Bd., pp. 384, 385, Taf. 44, Fig. 22, 1911.
 McCRADY, J., "On the *Lingula pyramidata* described by Mr W. Stimpson," *Amer. Journ. Sci. and Arts*, 2 ser., vol. xxx, pp. 157, 158, 1860.
 MORSE, E. S., "Embryology of *Terebratulina*," *Mem. Boston Soc. Nat. Hist.*, vol. ii, pp. 249-264, 1873.
 MORSE, E. S., *Proc. Boston Soc. Nat. Hist.*, vol. xix, p. 266, 1878.
 MÜLLER, F., "Beschreibung einer Brachiopodenlarve," *Archiv f. Anat. Physiol.*, Jahrg. 1860, pp. 72-80, Taf. i.
 MÜLLER, F., "Die Brachiopodenlarve von Santa Catharina," *Archiv f. Naturgesch.*, Jahrg. xxvii, Bd. i, pp. 53-56, 1861.
 SEMPER, C., "Reisebericht," *Zeitschr. wiss. Zool.*, Bd. xi, pp. 103, 104, 1861; Bd. xiv, p. 424, 1864.
 SEWELL, R. B. S., "Note on the Development of the Larva of *Lingula*," *Records Indian Mus.*, vol. vii, pp. 88-90, 1912.

* Except the abnormal specimen mentioned on p. 62, which has only three cirri on the left side.

- SIMROTH, H., "Die Brachiopoden der Plankton-Exped.," *Ergebn. Plankton-Exped.*, Bd. ii, F.f., 19 pp. 1 Taf., 1897.
- YATSU, N., "On the Development of *Lingula anatina*," *Journ. Coll. Sci. Imp. Univ. Tokyo*, vol. xvii, art. 4, 112 pp., 8 pls., 1902.
- YATSU, N., "Notes on Histology of *Lingula anatina*," *op. cit.*, art. 5, 29 pp. 2 pls., 1902a.
- YATSU, N., "Notes on the young *Discinisca*," *Zool. Anz.*, Bd. xxix, pp. 561-563, 1905.

DESCRIPTION OF THE PLATES.

List of Reference Letters.

- | | |
|---|---------------------------------------|
| A. Anus. | M.G. Mid-gut. |
| A.S. Arm-sinus. | M.M. Mantle-margin. |
| B.M. Brachial muscle. | M.M.D. Margin of dorsal mantle. |
| B.M.T. Transverse brachial muscle. | M.M.V. Margin of ventral mantle. |
| B.W. Wall of body proper. | Mo. Mouth. |
| C. Cirrus. | M.T. Thickened area of mantle. |
| C1, C4, C11, C13. First, fourth, eleventh, thirteenth cirrus. | N.T. Nervous tract. |
| C.D. Cœlomoduct. | Œ. Œsophagus. |
| CH. Chæta. | O.A. Anterior ocluser muscle. |
| CH. I, CH. II, CH. III, CH. IV, CH. V. First to fifth large chætae of <i>Pelagodiscus</i> . | O.I. Obliquus internus muscle. |
| CH. S. Slender chætae. | O.P. Posterior ocluser muscle. |
| Co. Cœlom. | P. Pigment. |
| Co. E. Cœlomic epithelium. | P.D. Dorsal protegulum. |
| D.B. Dorsal blood-vessel. | PE. Peduncle. |
| D.M. Dorsal mesentery. | PE. E. Epithelium of peduncle. |
| E. Epistome. | PE. M. Muscles of peduncle. |
| G.C. Gland-cells in mantle. | PR. Periostracum. |
| G.L. Lateral nerve-ganglion. | P.S. Pigment-spot ("eye"). |
| G.P. Gastro-parietal band. | P.V. Ventral protegulum. |
| G.V. Ventral nerve-ganglion. | S. Shell. |
| H.L. Hinge line. | Sc. Statocyst. |
| IN. Intestine. | S.M. Shell-margin. |
| L.A.D. Anterior dorsal lobe of "liver." | S.M.D. Margin of dorsal shell-valve. |
| L.M. Lateralis muscle. | S.M.V. Margin of ventral shell-valve. |
| L.P.D. Posterior dorsal lob of "liver." | S.S. Supporting substance. |
| L.V. Ventral lobe of "liver." | St. Stomach. |
| M. Mantle. | T. Tentacle. |
| | T.M. Transverse muscles. |

PLATE IV.

Lingula anatina Bruguière.

Figs. 1, 2. Outlines of ventral (fig. 1) and dorsal (fig. 2) shell-valves of youngest larva obtained (52 mm. long). The protegulum, or primary shell, is seen in each valve. See p. 48. ($\times 39$.)

Fig. 3. Outline of ventral shell-valve of a larva 1.1 mm. long (larva c, group iii, p. 49). ($\times 39$.)

Fig. 4. Outer surface of the ventral valve of the largest larva, 1.6 mm. long (larva *d*, group v, p. 52); to show the protegulum and the principal growth-lines on the secondary shell. See p. 53. ($\times 39$.)

Fig. 5. Larva with 11 pairs of cirri, ventral aspect; drawn from a preserved specimen. The anterior and posterior oclusors and the lateralis muscle are shown, but the other muscles have been omitted. The cœlomoduets were present, but have not been shown; they are more clearly seen in later stages (see fig. 10). The cirri are contracted, and the mantle, which in life extends to the margin of the shell-valves, has also been withdrawn. The right and left lobes of the ventral "liver" are seen to unite in front and to open into the stomach by a common portion (see also fig. 10). Between the posterior margin of the lophophore and the anterior edge of the ventral nerve-ganglion in the body-wall there is a deep depression shown in light tone in the figure. Note the first indication of the peduncle. See p. 49. ($\times 90$.)

Fig. 6. Posterior end of a larva with 14 pairs of cirri (larva *a*, group v, p. 52), ventral aspect. Note the peduncle arising from the ventral mantle-fold, turning to the animal's right, then dorsally and left, and terminating in a knob lying between the dorsal and ventral mantle-folds. The narrow canal connecting the peduncular cavity with the cœlom is indicated. In the mantle on each side are chætæ and a series of gland-cells. Two of the chætæ—those first formed—are rather larger than the rest. The dark central area indicates the extent of the body proper. ($\times 90$.)

Fig. 7. The distal half of one of the large chætæ of a larva with 15 pairs of cirri (larva *d*, group v, p. 52). ($\times 500$.)

Fig. 8. Horizontal section of the dorsal region of a larva (*f*, group iv, p. 50) with 13 pairs of cirri. In the posterior part the section contains the dorsal body-wall (which is intact) in the anterior region of which are the two statocysts. Further forward the dorsal body-wall has been cut away. The two antero-dorsal "liver"-lobes are coming together in the middle line preparatory to opening into the stomach. The dorsal blood-vessel is seen through the dorsal body-wall, and a small portion of the vessel is cut again further forward in the dorsal mesentery. ($\times 100$.)

Fig. 9. Horizontal section, 20μ thick, of the same larva, taken nearly midway between dorsal and ventral surfaces. The section passes through the œsophagus and stomach and the postero-dorsal "liver"-lobes. The cirri are drawn only in outline; note in the lophophore on each side a portion of the arm-sinus and of the band of supporting substance lateral to it. Only the basal half of the tentacle is present in the section. ($\times 100$.)

Fig. 10. Horizontal section, 50μ thick, of the body proper of the same larva, taken in the ventral region, showing the posterior portion of the stomach (cut tangentially), the intestine, the cœlomoduets (nephridia), and the ventral "liver." The median anterior portion of the "liver" leads into the stomach, which, in that area, lies immediately dorsal to the plane of the section. Note also the ventral nerve-ganglion in the anterior wall of the body. ($\times 100$.)

PLATE V.

Pelagodiscus (Discinisca) atlanticus (King).

Fig. 11. Larva, ventral aspect. Between the posterior margin of the lophophore and the anterior edge of the body-wall there is a deep depression (*cf.* fig. 17). The dark tone on the mid-gut indicates the area occupied by the flagellated cells, *i.e.* the area which will form the chief part of the stomach. Note the intestine, cœlomoduets (nephridia), and peduncle. The five principal chætæ are shown on both sides; but on the right of the figure only are represented the three jointed chætæ which are situated in the ventral mantle-fold, and the first two and the last of the series of about thirty slender chætæ present in the dorsal mantle-fold. The mantle, which extends to the margins of the shells, is extremely thin over the greater part of its extent, but its thickened zone (*cf.* fig. 17) is represented by the deeper tone. ($\times 180$.)

Fig. 12. Dorsal aspect of the same larva, showing only the body proper. Note especially the statocysts, and the "eyes." The thickening of the body-wall in front is due to the presence on each side in that region of the lateral nerve-ganglion. ($\times 180$.)

Fig. 13. Distal end of the first left chætæ. See p. 60. ($\times 800$.)

Fig. 14. The third principal chætæ. The processes are on its anterior margin. See p. 61. ($\times 800$.)

Fig. 15. The distal end of the fourth principal chætæ; note the absence of spines on its median margin. See p. 61. ($\times 800$.)

Fig. 16. Proximal portion (about two-fifths) of one of the three jointed chætæ in the ventral mantle-fold. See p. 61. ($\times 800$.)

Fig. 17. Sagittal section of a larva. Note that at the margins of the shell-valves the periostracum is turned in and continued for some distance over the mantle-fold. The surface of the periostracum is studded with minute points and is therefore shown dotted. The mantle is in contact with the inner surface of the shell, and, except over the body proper, is composed of two lamellæ; these are represented diagrammatically as two thin nucleated membranes, over the greater part of its area the mantle is very thin. See pp. 61-65. ($\times 450$.)

Fig. 18. Horizontal section of a larva passing through the middle of the pigment spot ("eye"), and through the statocyst of the right side. A portion of the outline of the right anterior oclusor muscle is shown by dotted lines. See pp. 63, 64. ($\times 700$.)

Fig. 19. Three cells from the postero-ventral wall of the mid-gut, *i.e.* cells of the future stomach. See p. 64. ($\times 1800$.)





